Mineral Composition of the Foliage in Relation to the Growth of Scots Pine

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THE NUMEROUS REPORTS of pronounced responses in tree growth to the application of mineral fertilizers suggest that such measures may possess distinct economic advantages in the amelioration of low quality forest sites. The problem arises as to how the nature and extent of existing mineral deficiencies may best be established. The direct approach of setting up field trials with various levels and combinations of fertilizers is time consuming and expensive. Nor have soil analyses proved as reliable in the assessment of site fertility for forest trees as perhaps for agricultural crops. With these difficulties in mind, many investigators have turned to foliar analysis in the hope that the mineral composition of the foliage might provide a more reliable guide to the presence and extent of a particular mineral deficiency.

The simplest and most common application of foliar analysis is based essentially on comparisons between normal healthy trees and trees suspected of being mineral deficient, on the assumption that a lower concentration of a particular nutrient in the latter indicates a deficiency in that nutrient. This method has been used to a considerable extent by Nemec (1938, 1940, 1942) and others, in the diagnosis of mineral disturbances assumed responsible for the poor growth of trees in established stands. Its validity depends to a large extent on whether suitable standards of comparison representing "normal" concentrations of the various nutrients can be established for that particular species; from a practical point of view it also requires that, over the deficient range at least, the concentration of a nutrient in the foliage and its availability in the soil are both positively related to growth.

A considerable amount of attention has been devoted to the concept of normal or optimal concentrations of particular nutrients, especially in connection with the establishment of sub-optimal or minimum concentrations corresponding to deficiency conditions but the situation is still rather controversial (Goodall and Gregory, 1947). It is generally recognized that the mineral composition of the foliage of trees is influenced not only by the availability of nutrients in the soil but also by the age of the tree, the age of the foliage (i.e. in conifers bearing more than one year's foliage), the location of the foliage in the crown and the time of sampling (for a review of these factors cf. Leyton, 1948; White, 1954; Tamm, 1955). Recognition of these sources of variation has led to the adoption of standardized techniques involving comparisons of foliage sampled at the same time from trees of similar age.

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Almost universal agreement has been reached in sampling current foliage collected at the end of the growing season when variation in composition with time is at a minimum. As yet there appears to be no generally accepted scheme for the location of samples in the crown; certain investigators prefer an average value representing the whole crown (Wallihan, 1944; White, 1954) whilst others restrict sampling to a particular position in the crown (Mitchell and Chandler, 1939; Leyton, 1954). Experimental evidence as to the relative merits of the different sampling methods for agricultural and horticultural crops has usually been based on proportional differences between plants at different levels of nutrition (Goodall and Gregory, 1947), but little information of this kind appears to be available for forest trees despite the obvious importance of this factor. The following investigation was intended in part to provide more information on this point, with the hope that the choice of material can be established on a firmer basis than would appear to exist at present.

Even if we assume that valid comparisons can be made between trees by sampling under identical conditions there still remains the problem of interpreting nutrient concentrations in terms of tree growth and nutrient availability in the soil. Because of the possibility of luxury consumption (*i.e.* nutrient uptake not accompanied by increased growth, thus leading to excessive concentrations in the tissues) a "normal" tree need not necessarily reflect optimum concentrations of the various nutrients, if such exist, so that simple comparisons between trees may lead to considerable errors in diagnosis. Furthermore there is some doubt as to the amount of significance which can be attached to the concentration of individual nutrients independent of the influence of other nutrients and of other growth factors. According to certain investigators (Macy, 1936; Ulrich, 1943) there is for each nutrient, more or less independent of other growth factors, a narrow range of concentration (so called critical level) above which there is no response and below which growth increases as the supply of that nutrient is increased. A somewhat similar approach has been adopted by Heiberg and White (1951) and by Stone (1953) for forest trees in so far as they postulate certain concentrations of potassium and magnesium in the needles which correspond to deficiency levels of these nutrients. From investigations into the response of various hardwood species on different sites to various levels of a nitrogenous fertilizer, Mitchell and Chandler (1939) also suggest certain concentration ranges of this nutrient equivalent to minimum and optimum levels. On the other hand it has been claimed for agricultural crops (Lundegårdh, 1941) that the increment in yield following a given fertilizer application to plants with a particular concentration of that nutrient is markedly affected by the level of other nutrients, whilst Thomas (1945) maintains that the question of balance between nutrients must also be taken in account.

To a certain extent these difficulties in interpretation can be avoided by extending the investigations to cover a wide range of conditions of growth and nutrient status to allow for a statistical analysis of the relationships involved. From the investigations of Mitchell (1939) and Mitchell and Chandler (1939) in which trees (or seedlings) have been treated with different levels of a particular nutrient, it would appear that over the deficient range (i.e. the range over which growth increases as the nutrient supply is increased) there is a positive relation between nutrient supply, nutrient concentration in the foliage and growth and that over a more limited range this relationship is effectively linear. Experiments in the field with rubber (Chapman, 1941) and with Sitka spruce (Leyton, 1954) would confirm that a significant linear correlation between growth and the concentration of a particular nutrient in the foliage indicates a deficiency in that nu-

trient. According to the latter investigation it would also appear that actual fertilizer trials are not always necessary to provide the required range of material; even-aged stands showing heterogeneous growth conditions may also be used though of course the ultimate proof of deductions based on this material can only be obtained by applying the particular fertilizer and noting the response in tree growth. In analyses of this kind, attention is usually restricted to one particular nutrient (usually the so-called limiting nutrient), but in view of repeated observations that growth may be increased by the application of more than one nutrient (often with pronounced interactions), it would appear necessary to extend the analyses to include a number of nutrients, ideally all nutrient factors. Although a certain amount of work has been devoted to the effect of various nutrient combinations on tree growth (cf. Van Goor, 1953), few attempts have been made to relate these responses to nutrient concentration by means of multiple regressions. A limited example of this approach is provided by Stone (1953) for potassium and magnesium in red pine, and a more comprehensive analysis by Leyton (1955) for nitrogen, potassium, phosphorus, calcium and other ash constituents in Japanese larch. A similar comprehensive analytical approach has been adopted in the present investigation with Scots pine (*Pinus sylvestris* L.).

For the most part, investigations dealing with adult trees in the field have dealt with tree height or diameter as an expression of growth vigor and response. Since in the present investigation, data are available for dry weight production of the trees besides those for height and diameter, the analysis of growth-nutrient relationships has been extended to include dry weight.

Description of Experiment

Sample trees were selected from a pure plantation established in 1945 in the Bramshill forest, Berkshire, England. The soil is a sandy heathland podzol, overlying Barton beds (Eocene) with a dominant ground vegetation of common heather (*Calluna vulgaris*, L.) with bell heather (*Erica cinerea*, L.). The plantation is approximately 300 ft. above sea level and the average annual rainfall is 25-30 inches.

Ten trees were located within a radius of approximately 150 ft. ranging in height from 4.3 to 14.0 ft.; these trees represented roughly the range in height which occurred in the plantation as a whole and, in the absence of suppression by shade, the variation in vigor might be ascribed to a combination of heterogeneity in soil conditions and planting stock and perhaps to differences in treatment during planting. On the 5th of October, 1954, one lateral branch from each of the topmost three whorls of each tree (south side) was removed. At the same time, height and basal diameter were measured. The day after sampling, all needles were removed from the main stem of each branch, separated according to age and dried in an oven at 105° C. for 48 hours. After grinding in a mill, the needles were analyzed for nitrogen, phosphorus, potassium, calcium and total ash contents, using more or less conventional methods of analysis.

Two weeks after the initial sampling, each tree was cut at ground level for the determination of total dry weight. At the same time further needle samples were taken for analysis from the leading shoot of each tree.

Results

The range in concentration covering the ten sample trees for each nutrient and for each position of sampling is given in Table 1. An attempt has been made to estimate ash constituents other than P, K and Ca by subtracting from the total ash contents, values equivalent to P_2O_7, K_2CO_3 and CaO. In the absence of precise information as to the composition of the ash, the resulting "ash residue" must of course be treated only as an approximation.

These findings more or less agree with those of previous investigators as far as the effect of location and age on needle composition is concerned (Nemec, 1948; White, 1954). With current needles the highest nutrient concentrations were generally found in the terminal shoots, but there were no consistent differences between shoots lower down the crown. With increasing needle age nutrient concentrations tended to fall except in the case of calcium and ash residue which reached their highest concentrations in the older needles.

The relationship between needle composition and tree height. Linear correlations have been calculated between tree height and the concentration of each nutrient for each needle sample; the corresponding correlation coefficients are given in Table 2.

Inspection of these coefficients indicates in a number of cases, significant linear relationships (or linear components of the relationships) between tree height and nutrient concentration in the needles. For the current needles from the uppermost shoots there is evidence for a linear relation with more than one nutrient (e.g. in the terminal shoot, with N, P and K) whereas for the lowest whorl sampled (Whorl 3) only one nutrient, Ca, is possibly related to height. With the exception of potassium, there is little evidence for such relationships in the case of the older needles.

In those cases where the linear correlation closely approaches or exceeds the 5 percent level of significance, the coefficient (b) for the linear regression of nutrient concentration on tree height has been calculated and the values also given in Table 2.

It is evident from these regression coefficients that, as far as nutrient concentration

TABLE 1. Range in concentration of nutrients in pine needles of different age sampled from various parts of the crown of trees of different height. All results expressed as percentage dry weight.

Needle Age	Location of Shoot[1]	N	P	K	Ca	A[2]
Current	Terminal	1.26-1.76	.14-.21	.73-1.46	.25-.39	.24- .63
Current	Whorl 1	1.06-1.39	.11-.16	.65-1.08	.19-.30	.09- .84
Current	Whorl 2	1.00-1.37	.10-.15	.64- .98	.22-.34	.01- .59
Current	Whorl 3	1.08-1.31	.07-.13	.72- .89	.23-.41	.26- .63
2 years	Whorl 2	0.98-1.19	.04-.11	.55- .92	.36-.70	.84-1.72
2 years	Whorl 3	0.97-1.32	.05-.11	.59- .92	.16-.27	.99-1.70
3 years	Whorl 3	0.94-1.11	.08-.11	.54- .89	.18-.31	.90-2.27

[1]Whorls are counted from the top of the crown.
[2]Ash residue (for details cf. text).

TABLE 2. Statistical data for relationship between tree height and nutrient concentration in needles.

Needle Age	Location of Shoot	Linear correlation coefficients N	P	K	Ca	A	Regression coefficients N	P	K	Ca	A
Current	Terminal	.785 ×	.731 ×	.679 ×	.255	.313	.043	.007	.059	.....	.....
Current	Whorl 1	.579 ×	.836 ×	.774 ×	—.185 ×	.729	.022	.005	.038	.....	.052
Current	Whorl 2	.602 ×	.796 ×	.691 ×	—.214	.385	.022	.004	.023	.....	.....
Current	Whorl 3	.185	—.097	.578 ×	.673	.607	.....	.....	.....	.011	.026
2 years	Whorl 2	.401 ·	.473 ×	.773	.386	.507	.....	.....	.027	.....	.....
2 years	Whorl 3	.386	.384 ×	.703	.248	.488	.....	.....	.023	.....	.....
3 years	Whorl 3	—.259	—.157	.522	.537	.576	.....	.....	.....	.....	.....

(For p = .01, r = .765; for p = .05, r = .632.)

is concerned, needles from the terminal shoot provide the greatest degree of differentiation between trees of different height and that, where comparisons are possible, this differentiation becomes less marked as one progresses down the crown or samples older needles.

The interpretation of relationships based on simple correlation coefficients is complicated by the possibility of interrelationships between individual nutrients. It is therefore of some interest to consider these relationships in terms of multiple regressions of tree height on nutrient concentration. If all nutrient factors are concerned, we can calculate in each case a multiple regression equation of the form:

$$Y = b_1N + b_2P + b_3K + b_4Ca + b_5A + k$$

where Y is the estimated tree height (ft.), and N, P, etc. are N, percent dry weight; P, percent dry weight, etc. Data for the partial regression coefficients b_1, b_2, b_3, etc., and the constants k are given in Table 3, together with the corresponding multiple regression coefficients, R (representing the correlation between actual and estimated heights) and the standard errors of the estimates, S.E.

According to these data it would seem that tree height can be related to the mineral composition of any of the needles sampled from the upper part of the crown, but that the accuracy of the estimates is greatest in the terminal needles and decreases as one descends the crown. Between the various needle samples, however, the nature of the function varies considerably; e.g. for the current needles, the coefficient for the N factor shows a progressive change from a positive value in the terminal shoots to a similar but negative value in Whorl 3.

TABLE 3. Data for multiple regressions of tree height on nutrient concentration in needles.

Needle Age	Location of Shoot	Partial regression coefficients b_1(N)	b_2(P)	b_3(K)	b_4(Ca)	b_5(A)	k	R	S.E. (ft.)
Current	Terminal	14.0	−36.4	8.4	0.6	5.7	−16.6	.972	1.12
Current	Whorl 1	11.4	−47.0	16.8	0.5	4.4	−15.1	.942	1.59
Current	Whorl 2	− 7.6	125.5	15.7	− 0.2	4.6	−12.0	.928	1.76
Current	Whorl 3	−14.9	28.9	33.1	−32.2	9.8	−15.4	.915	1.91
2 years	Whorl 2	14.5	4.9	22.5	−11.7	5.5	−24.6	.921	1.84
2 years	Whorl 3	2.6	61.4	16.5	−19.9	5.3	−14.6	.813	2.76
3 years	Whorl 3	−34.2	−16.8	15.4	4.2	3.3	29.0	.880	2.25

(For p = .01, R = .917; for p = .05, R = .811.)

TABLE 4. Test for significance of partial regression coefficients.

Needle Age	Location of Shoot	Values for "t" b_1(N)	b_2(P)	b_3(K)	b_4(Ca)	b_5(A)
Current	Terminal	3.73	1.14	3.00	.06	* 2.17
Current	Whorl 1	1.67	.52	2.39	.02	.84
Current	Whorl 2	.82	2.57	2.21	.01	1.20
Current	Whorl 3	1.39	.47	1.78	1.74	1.68
2 years	Whorl 2	.64	.12	3.10	1.17	1.45
2 years	Whorl 3	.26	1.03	1.62	.65	.87
3 years	Whorl 3	1.58	.20	2.26	.10	.70

(For p > .05, t > 2.78.)

These regression equations of course give no direct information as to the significance of the contributions made by the individual nutrient factors. Such information may be obtained by calculating the standard error for each partial regression coefficient and testing for significance by applying the "t" test. The results of these tests are summarized in Table 4.

Despite the suggestions of significant multiple regressions of tree height on nutrient concentration in all needle samples (Table 3) it would appear from these "t" tests that in only two cases are the individual nutrients associated with significant (5%) partial regression coefficients viz. N and K in the terminal needles and K only in the two year old needles from Whorl 2. Evidently the existence of significant simple correlations between tree height and the concentration of a particular nutrient does not necessarily imply a significant contribution of that nutrient to the multiple regression. In many cases this must be due to significant interrelationships between individual nutrients e.g. in the terminal needles, P is significantly correlated with tree height but this is apparently a reflection of the K relationship since K and P are significantly correlated with each other ($r = .835$) and only K makes a significant contribution to the regression. It is also evident that a significant multiple correlation, as for example in the case of the needles from Whorl 1 (cf. Table 3), does not necessarily imply the existence of significant contributions from any of the individual nutrients. Again it is possible that the overall relationship between tree height and needle composition is influenced by interrelationships between individual nutrients.

In the case of the needles from the terminal shoots, the regression analysis can be modified to exclude all factors other than N and K since only these two nutrients are associated with significant partial regression coefficients. The new regression equation is:

$$Y = 11.79\ N + 5.70\ K - 10.18$$

yielding a highly significant multiple correlation coefficient of $R = .919$ and a standard error of ± 1.41 feet.

The relationship between needle composition and dry weight production. Data for the total dry weights of the above ground parts of each tree are given below together with the corresponding tree heights:

Tree ht. (ft.)	4.3	3.5	6.0	7.0	8.5	
	9.5	10.0	11.0	12.5	14.0	
Dry wt. (kg.)	.54	.38	.71	.73	1.59	
	2.41	2.56	4.48	7.56	6.95	

Analysis of these data reveals a highly significant linear component of the relationship between height and dry weight ($r = 0.929$) and it might be expected therefore that dry weight can also be related to needle composition. This is confirmed, for the current needles at least, by the multiple regressions, data for which are presented in Table 5.

Though still significant, the multiple correlation coefficients for dry weight are a little lower than those for tree height (cf. Table 3) and the estimates, therefore, correspondingly less precise. The partial regression coefficients for individual nutrients also differ from those relating to height but not so greatly as to suggest a fundamentally different kind of relationship. This view is supported by the "t" values for the various regression coefficients which again indicate the significance of the contributions made by the N and K factors in the terminal needles. There is also some suggestion that the same two nutrient factors are mainly concerned in the regression based on the needles from Whorl 1, a situation which is much less apparent from the corresponding height data (cf. Table 4).

Discussion and Conclusions

One of the main factors determining the choice of material for foliar analysis is the degree of differentiation obtained between plants of different growth vigor. Insofar as the deductions based on the present experimental material are valid, it would appear

TABLE 5. Data for multiple regression of above ground dry weight on nutrient concentration in current needles.

	N		P		K		Ca		A		
	b_1	t	b_2	t	b_3	t	b_4	t	b_5	t	R
Terminal	16.01	*3.95	—73.1	2.13	8.6	*2.85	— 7.9	.76	5.5	1.96	.954
Whorl 1	17.0	2.46	—88.4	.89	18.8	2.65	13.9	.63	1.2	.22	.916
Whorl 2	— 6.1	.51	90.6	1.43	12.5	1.36	12.9	.60	4.3	.87	.820
Whorl 3	— 7.2	.55	—41.3	.55	7.9	.35	36.8	1.64	4.5	.64	.815

b_1, b_2, etc. = partial regression coefficients
t = corresponding "t" value
R = multiple correlation coefficient

that the most suitable material is provided by needles from the terminal shoot. In practice of course this method of sampling is not possible if normal tree growth is to be maintained and under such circumstances, sampling is then best restricted to the current needles from the topmost lateral shoot. Current needles lower down the crown, or older needles, provide a much poorer basis for differentiation whilst samples representative of the whole crown may lead to completely different conclusions. This may be one of the reasons why previous investigators (e.g. Aaltonen, 1950) have been led to reject foliar analysis as a reliable guide to nutrient availability.

As regards the subsequent analysis of the relationship between tree growth and needle composition it must be emphasized that the interpretation of the results in terms of nutrient deficiencies rests on a number of assumptions, direct proof of which has not been put forward in this investigation. Basic to this particular approach is the assumption that the selection of trees of varying height in an even-aged plantation constitutes a valid sample. Besides heterogeneity in soil conditions, there are a number of other possible factors (genetic, planting stock vigor, treatment during planting, etc.) which would ultimately result in uneven growth and there is therefore no direct proof of a causal relationship between nutrient supply and growth, no matter how closely growth is related to the nutrient status of the foliage. The argument has been presented that a significant linear correlation between tree growth and the concentration of a particular nutrient in the needles implies a deficiency in that nutrient insofar as an increased concentration of that nutrient is then associated with increased growth. In practice, however, this assumes that increased concentrations in the needles can be brought about by increased supply via the soil and though previous investigations have shown this to be generally true under conditions of a deficiency of one nutrient (Mitchell, 1939; Mitchell and Chandler, 1939; Heiberg and White, 1951) the interpretation becomes rather more complicated when more than one nutrient is related to growth as in the present case with needles from the terminal shoots. Under these circumstances and because of possible interrelationships between nutrients, it seems logical to extend the analysis of the results to multiple regressions based on a number of nutrients. This approach implies that height is a function of nutrient status, a situation which can only be demonstrated by actual fertilizer trials in the field. It must also be emphasized that because of the small number of samples and the relatively large number of variables included in the regression, the statistical analysis should not be interpreted too strictly, especially when many of the variables are interrelated with each other. Nevertheless the fact that, in all cases, tree height can be significantly related to needle composition and that similar results have

been obtained elsewhere with another species using a much larger sample (Leyton, 1955) suggests that the observed relationships deserve a certain amount of attention. It has been shown for example that the terminal needles provide the closest agreement between actual and estimated heights (Table 3) and that the precision of the estimates tends to fall progressively as one samples lower down the crown. Within the limitations set by the investigation, this would confirm the advisability of sampling as near to the terminal shoot as possible. It would also appear in the case of the terminal shoot at least, that only nitrogen and potassium make significant contributions to the regression, and that the significant linear correlation between height and phosphate concentration result from the interrelationship of this nutrient with potassium. In the absence of actual fertilizer responses, the precise significance of these findings cannot be fully explained but the argument is tentatively put forward that the height growth of the trees is limited only by nitrogen and potassium insofar as only increased concentrations of these nutrients would be equivalent to increased growth. It must be admitted of course that the analyses give no indication as to how the concentration of these other nutrients will be affected by the addition of either nitrogen or potassium; theoretically, however, the relationship with height growth is independent of the concentration of other nutrients, provided that these remain within the range encountered in the present investigation; on this basis, therefore, only the interrelationship between nitrogen and potassium would appear to be involved. Experience with the growth of pines on comparable sites would confirm the presence of nitrogen deficiencies (Leyton, 1954) but as yet no evidence has been obtained for the presence of potassium deficiencies in these soils.

Since the total dry weight of the above ground parts of the trees was found to be closely related to height growth it was not surprising to find that dry weight could also be related to the nutrient composition of the needles with more or less similar results. This would suggest that, under these circumstances, height is a reasonably fundamental measure of growth.

Summary

Significant linear correlations have been established between the height growth of Scots pine growing in an even-aged plantation on heathland, and the concentration of various nutrients in needles of different age sampled from various parts of the crown; in the case of needles from the terminal shoots, nitrogen, phosphorus and potassium were all significantly related to growth.

The degree of differentiation between trees of different height, in terms of nutrient concentration in the current needles, was greatest in the terminal shoots and decreased progressively down the crown; with the exception of potassium, no differentiation was obtainable with older needles. It is suggested that current needles from as near the terminal shoot as possible provide the best material for foliar analysis.

For all needle samples, tree height can be significantly related to needle composition (N, P, K, Ca and other ash constituents) by means of multiple regression equations; the best estimate, with needles from the terminal shoot, yields a multiple correlation coefficient of 0.972 and a standard error of ± 1.12 feet. Tests on the partial regression coefficients for each nutrient suggest that, in the case of the terminal needles at least, only nitrogen and potassium make significant contributions to the regression; for these needles the function 11.79 N (% D.wt.) + 5.70 K (% D.wt.) — 10.18 provides an estimate of tree height with a standard error of ± 1.41 feet.

It is tentatively suggested from these results that the growth of the pines is limited by deficiencies in nitrogen and potassium insofar as increased concentrations of

these nutrients in the needles, independent of the concentrations of other nutrients within the range encountered, are associated with increased height growth.

A significant linear component has been established for the relationship between height and the total dry weight of the above ground parts of the trees. These dry weights can also be expressed in terms of regressions on nutrient concentration in the needles and the resulting functions more or less agree with those for tree height.

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